

A NEW GENUS AND SPECIES OF POLYNOID SCALEWORM COMMENSAL WITH *CHAETOPTERUS APPENDICULATUS* GRUBE FROM THE BANDA SEA (ANNELIDA: POLYCHAETA), WITH A REVIEW OF COMMENSALS OF CHAETOPTERIDAE

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ABSTRACT

A sexually mature commensal polynoid not referable to any known genus or species was found in the tube of a *Chaetopterus appendiculatus* Grube, 1874, from Ambon, the Banda Sea, Indonesia. The specimen is a complete male, characterized inter alia by 19 pairs of elytra on 46 segments; unusually enlarged, anteriorly directed anterior pair of eyes; numerous fine capillary notochaetae; numerous slender neurochaetae with long, slender hoods with transverse rows of elongated scales. A new genus and species are proposed for this taxon. The species is most similar to *Paralentia tonkinica* Uschakov, 1982, described from Hainan, South China Sea, which is herein transferred to the new genus. Commensals of Chaetopteridae are reviewed and a synoptic table of chaetopterid hosts (16 species in 5 genera) and symbionts (15 polychaete species + 19 decapod species, accidentals excluded) is given.

Scaleworms or polynoids are often associated with different groups of marine invertebrates (Pettibone, 1953, 1993; Paris, 1955; Clark, 1956; Britayev, 1981). No less than 39 species of polynoids are known to be associated with tube-dwelling polychaetes (Britayev and Martin, unpublished observations).

The tubes of chaetopterids probably offer one of the most "comfortable" habitats for commensals. Known inhabitants include decapods as well polychaetes, most of which are polynoids (Table 1). Up to now four species of polynoids were known to be associated with *Chaetopterus* spp., all from temperate waters (Table 1). A fifth species, *Lepidonotus squamatus*, has been found in empty tubes but not in occupied ones.

In connection with the senior author's study of a specimen of *Chaetopterus appendiculatus* Grube, 1874 from Ambon, Indonesia, we examined a small polynoid worm originally present in the tube and found it to differ from all known genera and species of polynoids. A new genus is proposed for this specimen, which is characterized inter alia by an unusually enlarged, anteriorly directed first pair of eyes and neurochaetae with long slender hoods. The genus and species are diagnosed and described herein and compared with related taxa, and the symbionts of chaetopterids are reviewed.

METHODS

The specimen has been studied by light- and scanning electron microscopy (SEM; parapodia only); all figures have been prepared with the aid of a Leitz camera lucida or from SEM photos. Parapodia for SEM were dehydrated through a graded ethanol series and in acetone, critical-point dried, mounted on aluminum stubs, sputter-coated with gold, and examined in a Jeol JSM-840 scanning electron microscope at the Zoological Museum, University of Copenhagen (ZMUC). The specimen (in alcohol) and permanent slides of removed or detached parapodia, elytra, sperm, etc. (mounted in Euparal) are deposited in Rijksmuseum Natuurlijke Historie, Leiden (RNHL), the Netherlands.

The synoptic table of symbionts of chaetopterids is mainly based on the literature. Crustacean nomenclature mainly follows Schmitt et al. (1973) for the pinnotherid crabs and that used in the cited papers for other groups, but Dr. Austin B. Williams, National Marine Fisheries Service, Washington, D.C., kindly reviewed all the decapods and brought to our attention two overlooked papers with generic revisions. Records of *Chaetopterus variopedatus*, earlier considered the only species in the genus, are placed under the species that appears most likely to be the correct one. Uncertain records are

Table 1. Some polychaete (*) and decapod symbionts of species of Chaetopteridae. ♦ = host originally as *Chaetopterus variopedatus*. Author and year are given only for first mention of each taxon.

Host and symbiont(s)	Locality	Reference
<i>Chaetopterus appendiculatus</i>		
Grube, 1874		
* <i>Ophthalmonoe pettiboneae</i> n. gen. and sp.	Banda Sea, Indonesia	This paper
<i>C. cautus</i> Marenzeller, 1879		
* <i>Harmothoe imbricata</i> (L., 1767)	Vostok Bay, Sea of Japan	Britayev, 1993
* <i>Pilargis berkeleyae</i> Monro, 1933	Vostok Bay, Sea of Japan	Britayev, 1993
<i>Pinnixa rathbuni</i> Sakai, 1934	Japan	Sakai, 1934–1965
<i>Pinnixa rathbuni</i>	Possjet Bay, S Siberia	Kobjakova, 1967
<i>Pinnixa rathbuni</i>	Vostok Bay, Sea of Japan	Britayev and Smurov, 1988 ♦; Britayev, 1993
<i>Polyonyx utinomii</i> Miyake, 1943	Tanosaki, Japan	Miyake, 1943 ♦
<i>Tritodynamia intermedia</i> Shen, 1935	Shantung Peninsula, China	Tu, 1938, host as “ <i>Chaetopterus</i> probably <i>C</i> <i>variopedatus</i> ”(1)
<i>Tritodynamia rathbuni</i> Shen, 1932	Japan	Sakai, 1934–1965, 1976
<i>Tritodynamia rathbuni</i>	Vostok Bay, Sea of Japan	Britayev, 1993
<i>C. insignis</i> Baird, 1864 (status uncertain, species may be distinct)		
* <i>Gattyana cirrhosa</i> (Pallas, 1766)	North Wales, UK	Williams, 1864, as “a <i>Polynoe</i> given in Mr. Gosse’s ‘Manual’”(2)
* <i>Gattyana cirrhosa</i>	Liverpool area, UK	Hornell, 1891, as <i>Nychia</i> <i>cirrosa</i>
* <i>Harmothoe longisetis</i> (Grube, 1863)	Liverpool area, UK	Hornell, 1891, as <i>Polynoe</i> <i>glabra</i> (H. Malmgreni Lankester, 1867)
<i>C. luteus</i> Stimpson, 1855 (status uncertain, probably distinct)		
<i>Polyonyx transversus</i> (Haswell, 1882)	Botany Bay, New South Wales	McNeill and Ward, 1930, host as <i>Chaetopterus</i> sp.
<i>Polyonyx transversus</i>	Careel Bay, Pittwater, NSW	Pope, 1946, confirmed by Peter Davie (in litt. to MEP 1996)
<i>C. norvegicus</i> Sars, 1835		
**Various nereids and the like”	Bergen Fjord, W Norway	Sars, 1835, in empty tubes
<i>C. pergamentaceus</i> Cuvier, 1830?		
* <i>Nereis</i> sp.	Beaufort, NC	Enders, 1905
<i>Pelia mutica</i> (Gibbes, 1850)	Cape Cod to Florida	Gray, 1961 ♦, crabs rare
<i>Pinnixa chaetopterana</i> Stimpson, 1860	Charleston Harbor, SC	Stimpson, 1860
<i>Pinnixa chaetopterana</i>	Long Island Sound, NY	Smith, 1880
<i>Pinnixa chaetopterana</i>	Beaufort, NC	Enders, 1905
<i>Pinnixa chaetopterana</i>	Woods Hole, MA	Pearse, 1913 ♦
<i>Pinnixa chaetopterana</i>	Cape Cod to Florida	MacGinitie and MacGinitie, 1949 ♦; Gray, 1961 ♦
<i>Pinnixa chaetopterana</i>	Chesapeake Bay, E USA	Lippson and Lippson, 1984 ♦

Table 1. Continued

Host and symbiont(s)	Locality	Reference
<i>Pinnixa chaetoptera</i>	Wellfleet, MA to Rio Grande do Sul, Brazil	Williams, 1965 ♦, 1984 ♦
<i>Polyonyx gibbesi</i> Haig, 1956 (= <i>Porcellana macrocheles</i> Gibbes, 1850)	Beaufort, NC	Enders, 1905, as <i>Polyonyx macrocheles</i>
<i>Polyonyx gibbesi</i>	US East Coast	MacGinitie and MacGinitie, 1949 ♦; Gray, 1961 ♦, both as <i>P. macrocheles</i>
<i>Polyonyx gibbesi</i>	Woods Hole, MA to Brazil?	Williams, 1965 ♦, 1984 ♦
<i>Polyonyx gibbesi</i>	N Gulf of Mexico	Gilbert, 1984 ♦
<i>Tumidotheres maculatus</i> (Say, 1818)	Beaufort, NC	Enders, 1905, as <i>Pinnotheres maculatus</i> ; Gray, 1961 ♦, as <i>P. maculatus</i> ; Campos, 1989, new genus
<i>Tumidotheres maculatus</i>	US East Coast	MacGinitie and MacGinitie, 1949 ♦, as <i>P. maculatus</i>
<i>Tumidotheres maculatus</i>	Off Martha's Vineyard, MA to Mar del Plata, Argentina	Williams, 1965 ♦, 1984 ♦, both as <i>P. maculatus</i> , "in tubes of <i>Chaetopterus variopedatus</i> "
<i>Tumidotheres maculatus</i>	Paraná, S. Sebastiao, Sao Paulo, Brazil	Costa, 1970, as <i>P. maculatus</i>
<i>Zaops ostreum</i> (Say, 1817)	Woods Hole, MA	Pearse, 1913 ♦, as <i>Pinnotheres ostreum</i> ; Manning, 1993, generic revision
<i>Zaops ostreum</i>	Cape Cod to Florida	Gray, 1961 ♦, as <i>P. ostreum</i>
<i>Zaops ostreum</i>	Salem, MA to Santa Catarina, Brazil	Williams, 1965, 1984, as <i>Pinnotheres ostreum</i> , "in <i>Chaetopterus</i> tubes"
<i>C. sarsii</i> Boeck, 1861		
* <i>Gattyana cirrhosa</i>	Trondhjem Fjord, Norway	Storm, 1881, as <i>Nychia cirrosa</i>
* <i>Lepidonotus squamatus</i> (L., 1758)	Trondhjem Fjord, Norway	Storm, 1881, in empty tubes
<i>C. variopedatus</i> (Renier, 1804)		
* <i>Gattyana cirrhosa</i>	Clare Island, Ireland	Southern, 1914
* <i>Gattyana cirrhosa</i>	[UK]	Paris, 1955, ref. to McIntosh
* <i>Gattyana cirrhosa</i>	Isle of Man, Irish Sea	Southward, 1956
* <i>Gattyana cirrhosa</i>	Salcombe, Devon, UK	Mettam, 1980
* <i>Harmothoe longisetis</i>	Mediterranean?	Fauvel, 1923, in tubes of chaetopterids
* <i>Harmothoe longisetis</i>	Mediterranean?	Paris, 1955, host as "le Chétopère"
<i>C. variopedatus</i> of authors, probably not Renier, 1804		
<i>Eulenia cometes</i> (Walker, 1887)	Singapore	Ng and Nakasone 1993, new genus for <i>Polyonyx cometes</i>
* <i>Malmgreniella baschi</i> Pettibone, 1993	E Pacific off S California	Pettibone, 1993; Ruff, 1995
<i>Opisthopus transversus</i> Rathbun, 1893	Monterey to San Diego, CA	Hopkins and Scanland, 1964
<i>Pinnixa bahamondei</i> Garth, 1957	Reloncavi, Chile	Garth, 1957
<i>Pinnixa tomentosa</i> Lockington, 1877	Monterey Bay, CA	MacGinitie, 1930, 1935
<i>Pinnixa transversalis</i> (H. Milne-Edwards and Lucas, 1844)	?	MacGinitie and MacGinitie, 1949

Table 1. Continued

Host and symbiont(s)	Locality	Reference
<i>Pinnixa transversalis</i>	[Probably Peru]	Garth, 1957
<i>Pinnixa transversalis</i>	Galapagos	Garth, 1946, 1960
<i>Pinnixa valdiviensis</i> Rathbun, 1907	Puerto Lagunas, Chile	Garth, 1957
<i>Polyonyx quadriungulatus</i> Glassell, 1935	Gulf of California, Mexico	Kudenov and Haig, 1974
<i>Chaetopterus</i> n. sp. (M.E. Petersen, in prep.)		
* <i>Gattyana</i> [<i>G. cirrhosa</i>]	Øresund, mud bottom, off DK	K. W. Ockelmann (pers. comm.)
<i>Chaetopterus</i> sp.		
* <i>Gattyana cirrhosa</i>	English Channel	Fauvel, 1923, ref. to "var. <i>Chaetopteri</i> " [sic], no author or host species given
* <i>Harmothoe areolata</i> (Grube, 1860)	British coast	McIntosh, 1900
* <i>Harmothoe areolata</i>	NE Atlantic	Fauvel, 1923
<i>Pinnixa transversalis</i>	San Lorenzo Isl., Peru	Rathbun, 1910; Garth, 1957
<i>Pinnixa transversalis</i>	Gulf of California	MacGinitie and MacGinitie, 1949, in tubes
<i>Polyonyx asiaticus</i> Shen, 1936	Chefoo, Shantung Peninsula	Shen, 1936, "Probably living in the tube of <i>Chaetopterus</i> ."
<i>Polyonyx sinensis</i> Stimpson, 1858	China Sea	Shen, 1936
<i>Polyonyx</i> sp.	W coast of Lower California	MacGinitie and MacGinitie, 1949, in tubes
<i>Zaops ostreum</i>	Salem, MA to State of Santa Catarina, Brazil	Williams, 1965, as <i>Pinnotheres</i> <i>depressus</i> ; Manning, 1993, generic revision
<i>Mesochaetopterus japonicus</i> Fujiwara, 1934		
<i>Tritodynamenia rathbuni</i>	Japan	Sakai, 1934–1965, 1976
<i>M. rickettsi</i> Berkeley and Berkeley, 1941		
* <i>Malmgreniella "lunulata"</i> [not Delle Chiaje, 1830]	Corona del Mar, southern California	Berkeley and Berkeley, 1941; Pettibone, 1953, both as <i>Harmothoe lunulata</i> (3)
<i>M. sagittarius</i> (Claparède, 1870)		
* <i>Lepidasthenia elegans</i> (Grube, 1840)	Solomon Islands	Gibbs, 1969, 1971
<i>Phyllochaetopterus herdmani</i> (Hornell in Willey, 1905)		
* <i>Lepidasthenia maculata</i> Potts, 1910	Solomon Islands	Gibbs, 1969, 1971
<i>P. prolifica</i> Potts, 1914		
* <i>Dorvillea pseudorubrovittata</i> Berkeley, 1927	Puget Sound, Washington	Staff of University of Washington, in litt. from anonymous referee
<i>Phyllochaetopterus</i> sp.		
* <i>Harmothoe brevipalpis</i> Bergström, 1916	Concepcion Bay, Chile	Cañete et al., 1993, in tubes

Table 1. Continued

Host and symbiont(s)	Locality	Reference
* <i>Telolepidasthenia loboto-biensis</i> Augener and Pettibone in Pettibone, 1970	Malay Archipelago, Philippine Islands	Pettibone, 1970
<i>Sasekumaria selangora</i> Rullier, 1976		
<i>Polyonyx vermicola</i> Ng and Sasekumar, 1993	Selangor, Peninsular Malaysia	Ng and Sasekumar, 1993, obligate commensal
<i>Spiochaetopterus challengeri</i> Caullery, 1944		
* <i>Lepidasthenia ocellata</i> (McIntosh, 1895)	Japan	Okuda, 1936; Clark, 1956

(1) By Sakai 1976 considered a junior synonym of *T. horvathi* Nobili, 1905, a commensal of **Loimia medusa* (Terebellidae). (2) Footnote by Baird says this is a variety of *Lepidonotus cirratus* [var. *parasiticus* Baird, 1864]; McIntosh 1900 refers it to *G. cirrosa*. (3) Pettibone (1993) transferred species of this group to *Malmgreniella* Harman, 1967, but does not seem to have treated the three specimens reported as commensals of *M. rickettsii* by Berkeley and Berkeley (1941), although one of the Berkeleys' four specimens, collected by MacGinitie from the burrow of a ghost shrimp, is described as a new species (*H. macginitiei* Pettibone, 1993). *M. lunulata* (Delle Chiaje, 1830) (type locality Mediterranean) has been indiscriminately used for a number of commensal polynoids; the southern California specimens are herein considered a similar species of as yet unknown identity.

noted as such and not referred elsewhere. This arrangement also groups species geographically; despite possible errors, we hope that it will make it easier to recheck the records when the opportunity arises. Only species large enough to harbor commensals and known or believed to be distinct are listed. Types of *Chaetopterus* are currently being reexamined, and redescriptions of many of these species are in preparation by the senior author.

SYSTEMATICS

Ophthalmonoe new genus

Type Species.—*Ophthalmonoe pettiboneae*, new species, by original designation herein. Gender: Feminine.

Diagnosis.—Segments up to 46. Elytra and elythrophones 17–19 pairs, on segments 2,4,5,7, alternate segments to 23,26,29,32,35,38,41,42. Elytra delicate, transparent, smooth except for micropapillae. Prostomium bilobed, bluntly rounded, without cephalic peaks, with 3 antennae, median antenna with ceratophore in anterior notch, with long style (*O. tonkinica*; missing on *O. pettiboneae*); lateral antennae with distinct ceratophores, arising ventrally, with short styles; 2 long palps; 2 pairs of eyes, anterior pair enlarged and directed anteriorly (*O. pettiboneae*) or similar in size to posterior pair and directed ventrally (*O. tonkinica*). Tentaculophores of segment 1 lateral to prostomium, without chaetae, with dorsal and ventral tentacular cirri similar to median antenna (*O. tonkinica*, missing in *O. pettiboneae*). Palps long, acuminate, smooth. Segment 2 (buccal segment) with first pair of elythrophones, biramous parapodia and buccal ventral cirri longer than following ventral cirri. Pharynx with 9 dorsal and 9 ventral large terminal papillae, with pair of jaws deep inside pharynx. Parapodia biramous, with smaller notopodium and larger neuropodium, both rami with projecting acicular lobes, notopodium with prolonged tapering prechaetal lobe; prechaetal lobe of neuropodium longer, with supraacicular process; postchaetal lobe shorter; both triangular. Notochaetae numerous fine capillaries with imperceptible ornamentation. Neurochaetae numerous, slender, with distally pointed internal part surrounded by long slender hood ornamented with transverse rows of slender scales; hood without distal opening. Dorsal cirri of nonelytragerous segments with cylindrical cirrophores and long

styles; ventral cirri short. Pygidium with two tapering anal cirri arising midventrally.

Etymology.—From Greek, *ophthalmos*, eye + *noe*, referring to the polynoid worm with large eyes.

Comparisons.—The subfamilial relationships of the genus are not quite clear, but only in Arctonoinae (Hanley, 1989) do we find hooded neurochaetae: both *Gastrolepidia* Schmarda, 1861 and *Asterophilia* Hanley, 1989 have hooded neurochaetae, but here the hoods are restricted to the tips of the chaetae, whereas in *Ophthalmonoe* the hoods extend along much of the free length of the chaetae and are ornamented with transverse rows of minute petaloid scales; moreover, both of the first two genera differ from *Ophthalmonoe* in the more posterior position of the anterior eyes and in lacking fine capillary notochaetae. They moreover differ in number of elytragerous segments: up to 31 in *Gastrolepidia*, 17–19 in *Ophthalmonoe*, and only 15 in *Asterophilia*.

One species of the genus *Holelepidella* Willey, 1905—*H. nigropunctata* (Horst, 1915) (redescribed by Pettibone, 1969)—might be confused with *Ophthalmonoe* in having 19 pairs of elytra and in the form of the parapodia. However, *Ophthalmonoe* is easily distinguished by the more anterior position of the anterior eyes, by having elytra on segments 29,32,35 (instead of 29,31,34,36 in *Holelepidella*) and by the presence of hooded neurochaetae.

The type species of *Paralentia* Uschakov, 1982, *Halosydna* (*Alentia*) *annamita* Fauvel, 1934, in which genus *O. tonkinica* was originally placed, differs significantly from *Ophthalmonoe* in the form of the parapodia, which are shorter and of a different shape, and in having short, broad and serrated neurochaetae instead of long, slender hooded ones.

The new genus is established for two species, both from the tropical west Pacific: *O. tonkinica* (Uschakov, 1982), new combination, and *O. pettiboneae*, new species.

Ophthalmonoe pettiboneae new species

Figures 1–3

Material Examined.—INDONESIA: Indonesian-Dutch Snellius-II Expedition, Banda Sea: Ambon, Poka, inner bay, Ship T, THEMA 4, Cruise 1, Stat. 4B, dive, 4 Sept 1984, 3–9 m (Holotype, RNHL No. 19700, 1 complete but broken (2 pieces) mature male in good condition, in tube of *Chaetopterus appendiculatus* Grube, 1874, collected by Harry A. ten Hove, ident. MEP). Note with specimen: "Symbiotic in tube of *Chaetopterus*."

Description.—Holotype a complete mature male in two pieces, most cirri and elytra present and attached. Body short, wide, flattened, with up to at least 46 segments (17 anterior + 29 posterior in holotype), 7 + 10.4 mm long = 17.4 mm total length (extended pharynx excluded), 7 mm wide at midlength with parapodia but without chaetae, 2.5 mm wide without parapodia. Gonads visible through parapodial walls from segment 11.

Prostomium (Fig. 1A, C) slightly wider than long, without detectable cephalic peaks, broadest at midlength (weakly hexagonal), bluntly rounded in front of anterior eyes. Ceratophore of median antenna in shallow median notch, with dark brown pigment ventrally and laterally; median antenna lost. Lateral antennae arising anteriorly, adjacent and slightly ventral to median antenna, of similar width throughout most of length, tapering slightly at tips, with subterminal ring of dark brown pigment. Palps long, acuminate, smooth, without pigment. Eyes 4, dark brown, with conspicuous, transversely oval lenses; anterior pair of eyes larger

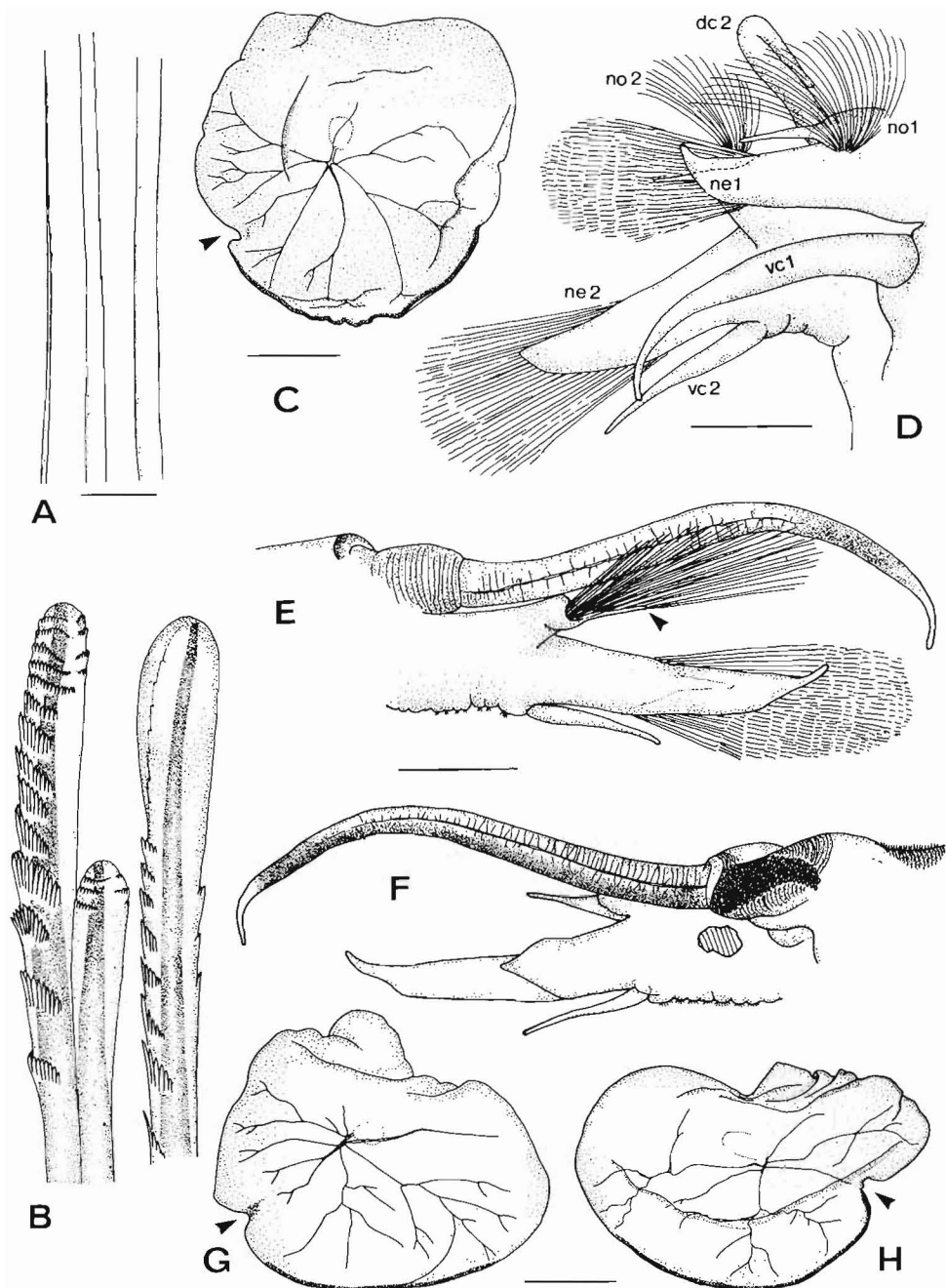


Figure 2. *Ophthalmonoe pettiboneae*, holotype: A. Tip, middle and base of notochaeta from left parapodium 20 as seen under oil immersion (see E, F). B. Neurochaetae from same. C. Left elytron from middle segment; notch (arrowed, also in G, H) at posterolateral margin fits around dorsal cirrus of succeeding segment. D. Right parapodia 1 and 2 (=segments 2 and 3), anterior view, elytron of parapodium 1 not visible. E. Left parapodium segment 20, anterior view; arrowhead indicating tip of notopodium. F. Same, posterior view; hatched area below cirrophore indicating damage; note difference in pigmentation of dorsal cirrus and cirrophore in the two views. G. Left elytron of slightly more posterior segment than in C. H. Right elytron of more posterior segment. Scales: A, B = 10 μ m; C, G, H = 1 mm; D = 0.34 mm; E, F = 0.66 mm. (dc, dorsal cirrus; ne, neuropodium; no, notopodium; vc, ventral cirrus; numbers refer to parapodia 1 and 2)

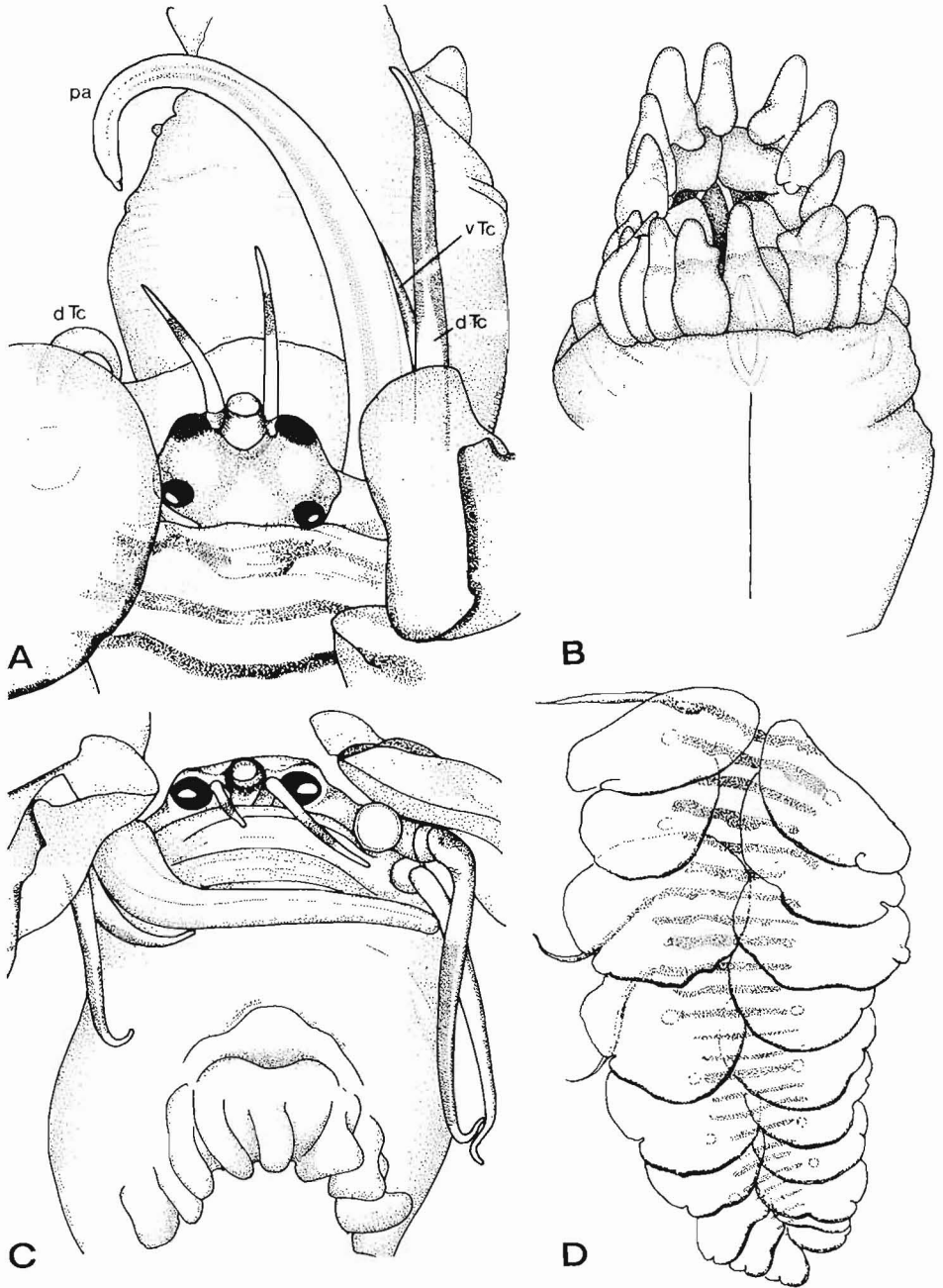


Figure 1. *Ophthalmonoe petuboneae*, holotype: A. Anterior end, dorsal view, with pharynx fully extended; median antenna and left palp missing, tentacular cirri of left side only partially visible. B. Extended pharynx, ventral view; ventral pair of jaws stippled. C. Anterior end, frontal view, left palp missing. D. Posterior fragment, dorsal view showing transverse banding, overlapping arrangement of elytra and posterolateral notches of elytra; parapodia and chaetae omitted (semidiagrammatic). Scales: A-C = 1 mm, D not to scale. (d Tc, dorsal tentacular cirrus; pa, palp; v Tc, ventral tentacular cirrus)

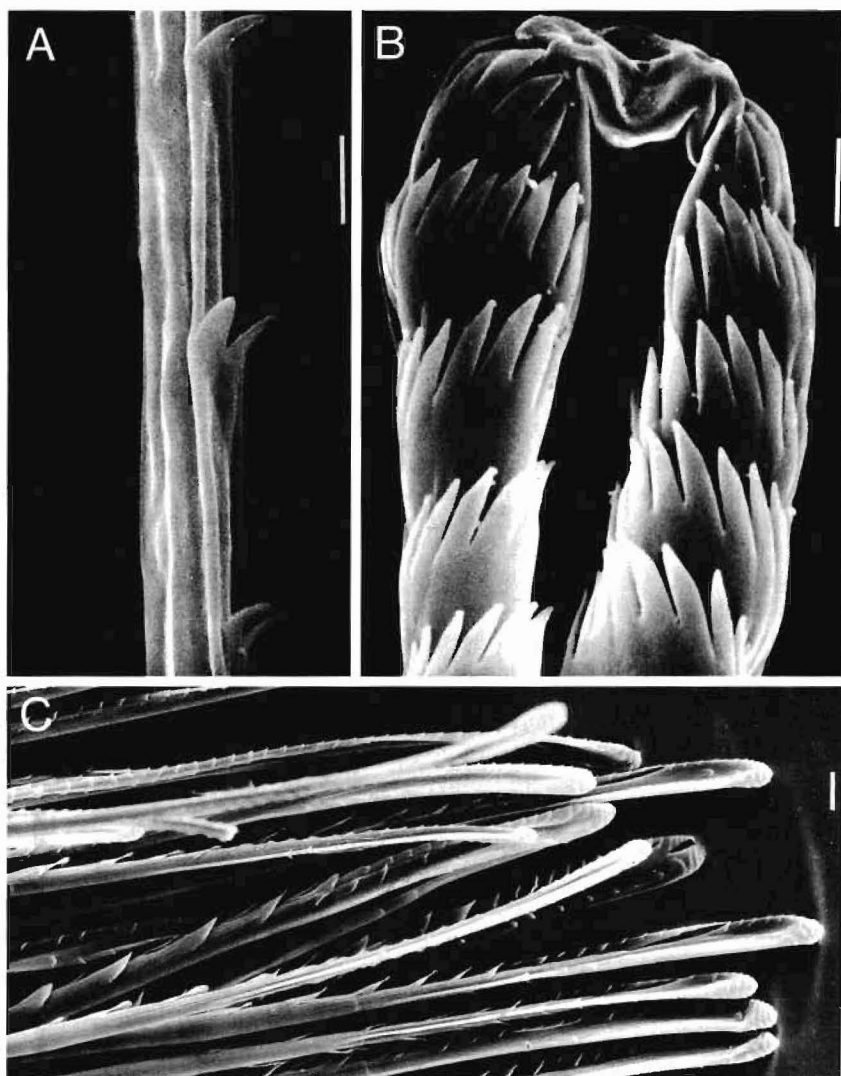


Figure 3. *Ophthalmonoe pettiboneae*, holotype. SEM photomicrographs of chaetae of midbody parapodium. A. Detail of notochaeta showing petaloid scales at right. B. Detail of tip of hood of one of ventralmost neurochaetae. Apparent opening is collapsed hood and not a real opening. C. Neurochaetae from lower part of fascicle. Note variation in size and number of rows of ornamentation. Arrowhead points at tear in hood. Scales: A, B = 1 μm ; C, 10 μm . (Photos A, B by Mats Bergius.)

(0.26 mm wide), about 1.4 times as wide as posterior pair (0.19 mm wide) and located at anterior edge of prostomium and directed anteriorly (not dorsally or ventrally, perhaps partly because pharynx is fully extended), visible through thin dorsal cuticle (Figs. 1–2); posterior pair smaller, at posterior edge of prostomium, directed dorsoposteriorly. Both pairs of eyes wider than long (length from front of lens to most posterior part of eye visible).

First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, without chaetae, with long dorsal and ventral tentacular cirri. Pharynx (Fig. 1B, C) extended, with 9 dorsal and 9 ventral large terminal papillae; pair of

jaws deep inside pharynx. Body relatively short and broad, widest around mid-length.

Elytra 19 pairs on segments 2,4,5,7, alternate segments to 23,26,29,32,35,38, 41,42; segments 43–44 with dorsal cirri; segments 45–46 very small and without elytra or dorsal cirri, without pigment. Elytra (Figs. 1D; 2C, G, H) firmly attached, all but a few still in place, those of right and left sides overlapping middorsally except for most anterior 3–4 pairs; all basically oval but markedly irregular in outline and often with folds, delicate, smooth except for evenly distributed micropapillae and transparent except for continuous, narrow dark brown rim along middorsal and posterior margins; venation distinct; most elytra with small but distinct notch on one side, just after pigmentation of rim ends, apparently where elytron fits around dorsal cirrus of following segment.

Middorsum (Fig. 1A, D) with conspicuous transverse dark brown band across each segment throughout length of body except for last few segments, on cirriferous segments continuing on posterior side of elytophores and dorsal cirri (Fig. 2E, F), on elytriferous segments stopping at bases of elytophores; anterior edge of band straight and sharply defined, posterior edge more irregular; short transverse bands of cilia laterally on anterior and posterior edges of pigmented band. Segment 5 additionally with transversely oval middorsal brown spot posterior to transverse band; following segments with bands slightly thicker middorsally. Other pigmentation absent.

Parapodia biramous (Fig. 2D–F), relatively long and slender in dorsal view, smooth; rich dark brown pigment on dorsal cirri (except distally) and posterior aspect of cirrophores; ventral cirri and cirrophores without pigment. Parapodia of segment 2 (chaetiger 1) small (Fig. 2D), about half as long as those of segment 3; notopodium small, short, with dorsal elytophore; notopodial acicular lobe short, rounded-triangular basally, with very slender, prolonged acicular process distally; neuropodium longer and larger than notopodium; prechaetal lobe of neuropodium elongate, distally triangular, distal part pointing dorsolaterally; postchaetal acicular lobe shorter, triangular; ventral (buccal) cirrus of segment 2 basally removed from neuropodium, arising a short distance ventral to this and slightly longer than neuropodium. Notopodia of segment 3 and following similar (Fig. 2D–F), shorter than neuropodium, with acicular lobe prolonged and tapering. Neuropodia with two widely spaced rows of cilia ventrally along length of parapodium; prechaetal lobe digitiform, much longer than triangular postchaetal lobe. Dorsal cirri: cirrophores and styles with rich dark brown pigment on posterior aspect, colorless and translucent to transparent on anterior aspect except for brown pigment subdistally; styles smooth, slender, tapering (not swollen basally), extending well beyond tip of neuropodial lobes. Ventral cirri of chaetigers 2 and following arising at midlength of parapodium, shorter than neuropodium, tapering, without pigment.

Chaetae colorless. Notochaetae (Figs. 2A, 3A) preacicular, numerous (more than 150), more slender than neurochaetae, exclusively fine, long, tapering capillaries appearing smooth at lower magnifications (e.g., 500 \times), and imperceptibly serrated along one edge under phase-contrast oil immersion (e.g., 1250 \times or higher; Fig. 2A), with “serrations” visible as slender petaloid scales under SEM (Fig. 3A, 15,000 \times). Neurochaetae (Figs. 2B, D, E; 3B, C) preacicular, numerous (well over 200 in right parapodium 15), in about 12–13 tiers, slender basally but thicker than notochaetae, becoming slightly broader at point where hood (and ornamentation) begins; internal part of chaeta unidentate, surrounded by long, slender hood along much of distal part; hood distally expanded, without any opening, in longer chaetae with up to at least 85 rows of close-set, narrow, petaloid spines (Figs. 2B; 3B,

C); rows of spines largest, most conspicuous and farthest apart at base of chaeta, smaller and closer together distally, mainly on one side of chaeta, not continuous or spiraling.

Anus terminal, with two tapering anal cirri arising from midventral edge of pygidium.

Distribution.—Pacific Ocean: Banda Sea, Ambon.

Etymology.—Named for Dr. Marian H. Pettibone, Zoologist Emeritus at the Smithsonian Institution, highly valued friend, and author of numerous important contributions on the taxonomy of scaleworms and many other polychaete groups.

Remarks.—*Ophthalmonoe pettiboneae* is very similar to *O. tonkinica* but differs in (1) the relative size and orientation of the anterior eyes, (2) the irregular shape and notches in the elytra, (3) the considerably greater number of the notochaetae, perhaps also (4) the smaller size of the notochaetae, and (5) the greater amount of pigmentation.

The anterior eyes are clearly larger than the posterior ones and directed anteriorly in *O. pettiboneae*, whereas the eyes are “approximately equal in size” with the anterior eyes “directed downward” in *O. tonkinica* (Uschakov, 1982: 143, pl. 47: fig. 3; size confirmed by Dr. G. N. Buzhinskaya). As the pharynx is fully extended on *O. pettiboneae*, it cannot be excluded that this is responsible for the difference in orientation of the eyes, but in a similar-sized *Harmothoe imbricata* (L., 1767), which also has the anterior eyes under the prostomium, a similar anterior orientation was not observed in a specimen with extended pharynx, and the eyes in this species are also relatively much smaller.

The shape of the elytra in *O. tonkinica* is not mentioned by Uschakov, who figures them as flat and regularly oval, without any posterolateral notch (Uschakov, 1982, pl. 47, fig. 6). In *O. pettiboneae* the elytra are not flat, but slightly ruffled, and it is nearly impossible to mount them without folds; although the posterolateral notch is easily overlooked when the elytra are examined in situ, it can be seen (Fig. 1D) and is difficult to overlook when an elytron is mounted on a slide, which is necessary for examination of papillae. Moreover, in *O. pettiboneae*, the posterior rim of dark pigment ends just before the notch (Fig. 2C, G, H), suggesting that both the pattern of elytral pigmentation and the notch are usual features.

Uschakov (1982) found “about 50” notochaetae in *O. tonkinica*; this has been confirmed by Dr. Buzhinskaya, who found 50–60; we found over 150 in a mid-body parapodium of *O. pettiboneae*. Uschakov (1982) further states that the notochaetae of his species are larger than in *Paralentia annamita*; the notochaeta figured by Fauvel (1934, 1935, fig. 1f in both) appears to be considerably wider than in *O. pettiboneae*. Given the exceedingly small diameter of the notochaetae of *O. pettiboneae*, it is hard to imagine their being described as larger than those of another species, and Uschakov’s specimen is slightly smaller than ours: 5.5 mm greatest width with parapodia, 1.7 mm without (measured between bases of parapodia). We find this to be further support for specific distinctness.

The greater amount of pigmentation in *O. pettiboneae* cannot be evaluated without more material and might be part of a cline, or simply intraspecific variation within a population. Observed differences are pigmentation of lateral antennae, tentacular cirri and elytra in *O. pettiboneae* versus no pigment here in *O. tonkinica*. Similarly, the larger number of elytra cannot be evaluated on the present material, as the single specimen of *O. pettiboneae* is slightly larger and has more segments than reported for *O. tonkinica*; as the distribution of elytra is otherwise

identical in the two species, larger specimens of *O. tonkinica* are necessary to determine if a difference is present.

Biology.—Much of the specimen is covered with clumps of mature sperm. These are of primitive type, with a round head about 1.3 μm in greatest diameter (measured on a Euparal mount), a very inconspicuous acrosome (appears to be cap-like, but not seen very clearly under phase-contrast oil immersion with 1,250 \times magnification), and what seem to be 4 mitochondria. The sperm cannot be from the chaetopterid host, as the latter is a female.

Ophthalmonoe tonkinica (Uschakov, 1982), new combination

Paralentia tonkinica Uschakov, 1982: 141–142, pl. 47, figs. 3–6.

Remarks.—The type material from Hsing-ying, Hainan Island, South China Sea, 11–13 m depth, was not examined by us, but is well described by Uschakov (1982), who unfortunately gave no information about habitat. Dr. Galina N. Buzhinskaya kindly reexamined the specimens, confirmed that the description is correct, and checked some points about which we were in doubt (see above).

Originally placed in *Paralentia* Uschakov, 1982, *O. tonkinica* differs significantly from the type species of *Paralentia*, *Halosydna (Alentia) annamita* Fauvel, 1934, in the form of the parapodia and chaetae and is more closely related to *O. pettiboneae* in having prolonged tapering parapodial lobes, numerous fine notochaetae, hooded neurochaetae, and smooth and delicate elytra. The species are compared under *O. pettiboneae*.

DISCUSSION

Delicate and transparent elytra probably are a “commensal” feature of this species. Such elytra are typical for some other commensal scaleworms (*Malmgreniella*, *Gastrolepidia*, *Hololepidella*). Another commensal feature is the enlarged anterior pair of eyes, directed anteriorly and with conspicuous lenses. This orientation and structure of the eyes are rather rare among polynoids, but are typical for tube-dwelling acoetids (= polyodontids), another family of scaleworms. Therefore it seems likely that the anteriorly directed and enlarged eyes of *O. pettiboneae* are an adaptation to inhabiting worm tubes. The utility of hooded neurochaetae is not clear, but the other species in which they occur are also commensals.

The hoods of the neurochaetae are unusual in lacking an opening and in having surface ornamentation. Hanley's (1989) figures suggest that this is also the case in *Gastrolepidia* and *Asterophilia*. This does not appear to be known for other families in which hooded chaetae are found (e.g., Spionidae, Magelonidae, Capitellidae), and it seems unlikely that the hoods are homologous with ones in these families.

As can be seen from Table 1, polynoid scaleworms are the dominant group of polychaete symbionts of chaetopterid tubes (13 out of 15 species of polychaetes, but 1 of the 13 has only been reported from empty tubes), but they are greatly outnumbered by pinnotherid and other small crabs (21 species, 20 of which symbionts of *Chaetopterus* spp., 1 of the 20 probably accidental [*Pelia mutica*]). As species of *Chaetopterus* are those with the largest tubes, it is not surprising that symbionts of this genus are predominantly crabs, whereas symbionts of chaetopterids in more close-fitting, slender tubes are generally polychaetes. One other factor that may play a role is the shape of the tube: basically U-shaped and open at both ends in *Chaetopterus* and straight or J-shaped, with one end usually bur-

ied in the substrate in the other genera. As far as we know, these differences have not been investigated. Moreover, while a number of the crabs appear to be obligate commensals, this does not appear to be the case with the polychaetes, most [all?] of which can be found free-living or with other hosts.

Because of the common belief that *Chaetopterus* is a monotypic genus with a single variable species, *C. variopedatus*, it is likely that some of the host records are incorrectly referred. Although most of the material has not been examined, based on literature and as yet limited knowledge of species present in the areas, an attempt has been made to group the hosts records under the most likely possibility, as this seemed more useful than placing the majority of them under *C. variopedatus*. Thus, records from the Sea of Japan have been referred to *C. cautus*, which to date is the only larger infaunal species known to occur there; a smaller epifaunal species, also referred to *C. variopedatus* but not this, has not yet been reported to harbor commensals. A redescription of *C. cautus* will be published separately (Petersen, in prep.). *C. variopedatus* is not cosmopolitan or as widespread as commonly believed, and even along the North American East Coast, at least two and perhaps three distinct species have been (incorrectly) referred here (Petersen, 1984a, b). The material investigated by Gray (1961) was unfortunately not kept, but since the worms were taken from different bottom types, it is likely that two or more species were involved, at least one of which may be undescribed.

ACKNOWLEDGMENTS

This study was supported in part by the International Science Foundation (Grant No M3R 000) and the Russian Foundation "Biodiversity", both to T. A. Britayev. A travel grant from the Danish Carlsberg Foundation made it possible for M. E. Petersen to take part in the 5th International Polychaete Conference in Qingdao. H. A. ten Hove, Amsterdam, and J. van der Land, Leiden, arranged the loan of material; G. N. Buzhinskaya, Zoological Institute, St. Petersburg, provided additional information on the type material of *Paralentia tonkinica*; and K. W. Ockelmann, Marine Biological Laboratory, Helsingør gave us unpublished information on commensals of *Chaetopterus* n. sp. M. Bergius, Jeol (Skandinaviska) AB, Sweden, assisted MEP with some of the SEM photomicrographs and photographer G. Brovad (ZMUC) made the prints. J. B. Pearce and especially A. B. Williams, National Marine Fisheries Service, Woods Hole and Washington, D.C., respectively, kindly reviewed the decapods and provided references to several recent generic revisions. P. Davie, Queensland, checked the identity of Pope's (1946) report of *Polyonyx transversus*. Finally, we gratefully acknowledge the thoughtful comments of D. Reish and two anonymous referees, one of whom provided the information on *Dorvillea pseudorubrovittata* as a commensal of *Phyllochaetopterus prolifica* in Puget Sound, Washington.

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DATE ACCEPTED: October 11, 1996.

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